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Global Climate Change Leads to Mistimed Avian Reproduction

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I. SUMMARY

Climate change is apparent as an advancement of spring phenology. However, there is no *a priori* reason to expect that all components of food chains will shift their phenology at the same rate. This differential shift will lead to mistimed reproduction in many species, including seasonally breeding birds. We argue that climate change induced mistiming in avian reproduction occurs because there is a substantial period between the moment of decision making on when to reproduce and the moment at which selection operates on this decision. Climate change is therefore likely to differentially alter the environment of decision-making and the environment of selection. We discuss the potential consequences of such mistiming, and identify a number of ways in which either individual birds or bird populations potentially can adapt to reproductive mistiming.

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II. INTRODUCTION

Different aspects of global climate change, such as the increase in ambient temperature during the last 30 years, have been shown to influence a wide range of biological systems (Wuethrich, 2001; Walthers *et al.*, 2002). One important aspect of biological systems that has been affected by climate change is phenology, such as the timing of reproduction. For many avian species in the temperate zone, there is only a short period in the annual cycle when conditions are most suitable for reproduction. An increase in ambient temperature most likely leads to an advancement of optimal breeding conditions, and as a consequence birds are expected to advance their timing of reproduction.

The impact of climate change on timing of reproduction has frequently been reported in correlational studies which show that laying dates have advanced in the last decades in many bird species (Crick *et al.*, 1997; Crick and Sparks, 1999; Parmesan and Yohe, 2003; Root *et al.*, 2003; Dunn, 2004, this volume). However, recent investigations revealed considerable variation in responses of breeding time to climate change both within and among avian species (Dunn, 2004, this volume). Parmesan and Yohe (2003) reported that 78 out of 168 species of birds advanced their laying date (47%) but 14 (8%) showed a delay and the other 76 (45%) showed no significant change. Dunn and Winkler (1999) showed that tree swallows (*Tachycinta bicolor*) differ in the advancement of egg laying date across North America and Visser *et al.* (2003a) showed in a European wide comparative study that some great (*Parus major*) and blue tit (*P. caeruleus*) populations advanced their average onset of egg laying during the last 20 years, but others not (see also Figure 1a; Dunn, 2004, this volume, and Sanz (2002) for geographical variation in how the North Atlantic Oscillation (NAO) affects great and blue tit laying dates). Also laying date in *Ficedula* flycatchers differed across Europe, and this variation correlates very well with variation in changes in spring temperature; populations occurring in areas without warming of spring did not advance their laying date, while the more the local temperature increased the more the birds advanced their laying date over the years (Both *et al.*, 2004).

Clearly, there is variation both within and among species in how much, if at all, the timing of reproduction has advanced. The most relevant question is however not *whether or not* a population has advanced the timing of reproduction *per se*, but rather whether bird populations have shifted their timing of egg laying *sufficiently* to match the shift in the period of favourable conditions for raising chicks. This has been only rarely considered when reporting changes in timing of reproduction in the context of climate change. The few cases where advancement of both favourable breeding conditions and avian reproduction has been investigated show insufficient shifts in the timing of reproduction (great tit, Visser *et al.*, 1998, pied flycatcher, Both and Visser, 2001). These studies reported a mismatch between the time of maximum

availability of food for raising chicks and the time the chicks are fed by the parents (Figure 1). Within populations there have always been individuals that were mistimed, such as late arriving immigrant great tits which lay too late (Nager and van Noordwijk, 1995), or blue tits in evergreen forests which lay too early as a consequence of gene-flow from deciduous to evergreen habitat (Dias *et al.*, 1996; Blondel *et al.*, 2001). However, climate change weakens the

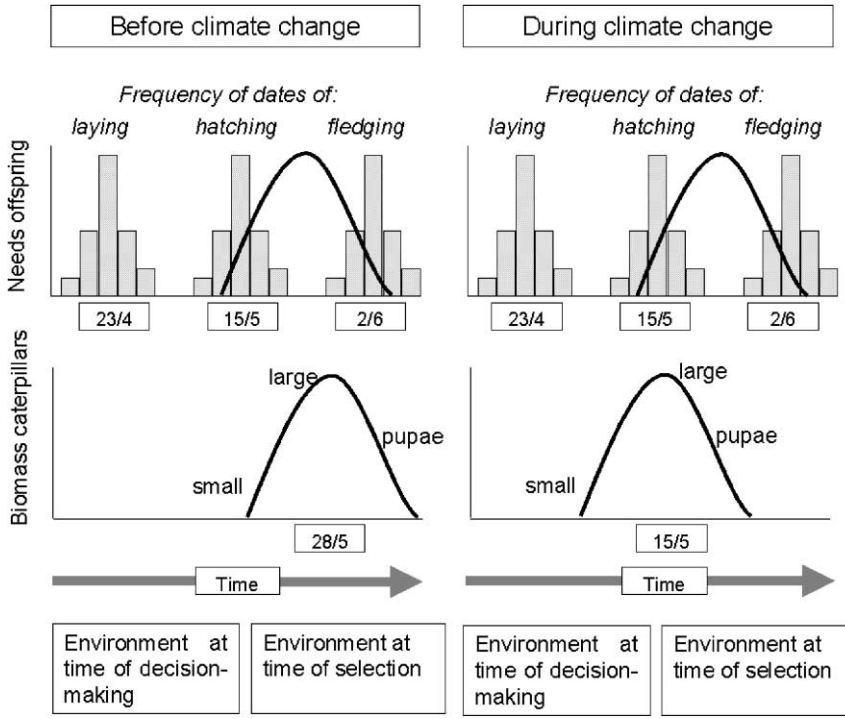

Figure 1 A graphical representation of reproductive mistiming due to climate change in Dutch great tits: left panels prior and right panels during climate change. Top panels represent the frequencies of (from left to right) laying dates, hatching dates and fledging dates. The need for food for the chicks in the nest is indicated with a solid line. Laying dates have not changed under climate change. Lower panels represent the biomass of defoliating caterpillar (main prey for the nestlings) availability: initially low as there are many, but very small, caterpillars, then a peak at the time when there are large caterpillars, followed by a decline when caterpillars start to pupate and are no longer available as prey. The peak date in caterpillar biomass shifts to an earlier date due to climate change, and there is no longer synchronisation between the time the nestlings are fed and maximum food abundance: the population is mistimed. Below the lower panels the environments of decision-making and selection are indicated (Figure 2).

synchronisation between food availability and offsprings' needs for the average individual in the population.

In this chapter we will explain why we expect that climate change in general will lead to reproductive mistiming in birds (Section III). Next, we will discuss the consequences of this mistiming for population numbers (Section IV) and how birds may adapt to mistiming, either via responses at the individual or population level (Section V). Throughout the chapter we will illustrate our arguments with our own research on blue tits, great tits and pied flycatchers, as reproductive mistiming in the context of climate change has most extensively been studied in these bird species.

III. WHY GLOBAL CLIMATE CHANGE WILL LEAD TO REPRODUCTIVE MISTIMING

Birds are adapted to year-to-year variation in the timing of favourable conditions, i.e., in general they lay earlier in warmer springs (Dunn, 2004, this volume). However, often birds cannot use direct measurements of abundance of the food fed to nestlings to time their reproduction, as gonad development and laying eggs occurs well before the date when chicks hatch. Therefore, birds need to use cues to time their laying date, i.e., environmental variables at the time of egg formation (the environment of decision-making). These cues should have a predictive value for when food is plentiful later in the season (the environment of selection that determines the contribution to the following generation, c.f. van Noordwijk and Muller, 1994). Different cues may be used, that are combined and weighted to produce a physiological response mechanism translating the cues from the environment into a laying date (Lambrechts and Visser, 1999). As the environment differs from year-to-year, and consequently the value of the cues differs, birds also lay at different times.

A serious but often ignored aspect of global climate change is that temperatures (or other weather variables) have not just simply increased, but that temperatures in some periods change at a different rate than in other periods, or that temperatures at different locations (wintering versus breeding area) are changing in a different way (Visser *et al.*, 1998, 2003b; Inouye *et al.*, 2000; Walthers *et al.*, 2002). This means that the cues (the environment of decision-making) are affected in a different way by climate change than the environmental variables that affect the timing of favourable conditions (the environment of selection), and that climate change will lead to mistiming, i.e., that the change in timing of the birds is unequal to the change in timing of their main food sources for chick feeding (Figure 2).

Next we will discuss how climate change will alter the environment of decision-making (Section A) and the environment of selection (Section B), and

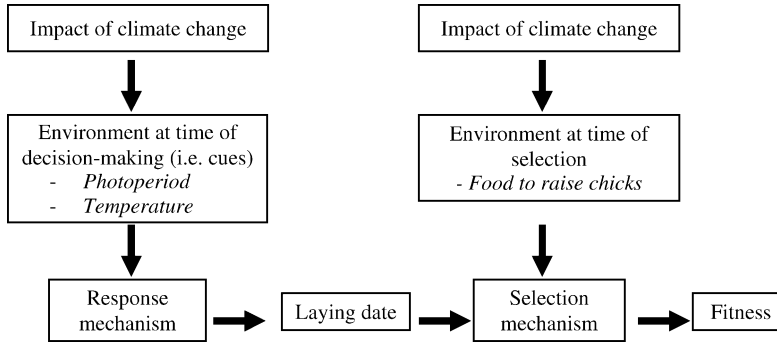

Figure 2 A schematic outline on how climate change may affect reproduction in birds. When the environment of decision-making is affected this may, via the response mechanism, affect laying date while changes in the environment of selection will affect the fitness consequences of laying dates.

therefore how it will influence the time that birds lay eggs and/or the conditions during which chicks are raised (Figure 2). We argue that there is no *a priori* reason why these two environments should change at the same rate in response to climate change, and why this likely leads to reproductive mistiming in birds (Section C).

A. Changes in the Environment of Decision-Making

Birds have to use those cues in the environment of decision-making that have some predictive value for the environment of selection in order to lay their eggs at the appropriate time (Wingfield *et al.*, 1992; van Noordwijk *et al.*, 1995). Climate change may well affect the environment of decision-making but assessing the magnitude of this effect is hampered by our deficient knowledge of the birds' response mechanism; which cues are used and how are these cues integrated to initiate gonadal growth and egg production. Only after this is known can we determine to what extent these cues are altered by climate change.

An important cue for the timing of reproduction is photoperiod as this sets the window within which reproduction will take place (Silverin *et al.*, 1993; Wingfield, 1993; Gwinner, 1996; Lambrechts and Perret, 2000; Sæther *et al.*, 2004, this volume). But as the change in photoperiod is the same every year, this cue cannot play a role in how birds adapt to year-to-year variation in optimal breeding time and thus additional cues should play a role. The fact that climate change will not affect such an important cue as day length may already limit the response in laying date to changes in climate. The strength of this effect depends

on how climate change influences the supplementary cues species use to time reproduction. Understanding adaptation to climate change thus should focus on these supplementary cues, although it is important to know how the effect of day length is constraining a response to climate change.

Ambient temperature is one of the most likely candidates for a supplementary cue. Many temperate zone species, including Great and Blue Tits, lay earlier in warmer springs (Kluyver, 1951; van Balen, 1973; Dhondt and Eyckerman, 1979; Perrins and McCleery, 1989; Dunn, 2004, this volume). However, to what extent gonad development and/or egg laying are directly sensitive to ambient temperature is unclear (Silverin, 1995, see for a review Visser and Lambrechts, 1999 and Dunn, 2004, this volume). The bud burst development of trees, which could serve as an accurate measure for the timing of the food peak does not play a direct role in the timing of gonad development and egg laying, as experimentally shown for great and blue Tits (Visser *et al.*, 2002).

Opportunistic breeders that breed after the start of a temporal unpredictable food supply do not have a window of reproduction set by photoperiod. They use cues that directly predict when food will be abundant, independent of calendar date. Zebra finches (*Taeniopygia guttata*) use flushes of grass seed as a cue, which themselves are directly related to the unpredictable incidence of effective rainfall (Zann, 1999). Also red crossbills (*Loxia curvirostra*, Hahn, 1998) and Piñon jays (*Gymnorhinus cyanoephalus*, Ligon, 1974) use the availability of their food supply directly to decide when to start egg laying. For these granivorous species there is a strong correlation between the environments of decision-making and selection, because of the highly predictable timing of their food supply at the time of egg laying. Therefore, they might be well able to cope with sudden changes in the timing of food availability due to climate change.

Long distance migrants have an extra handicap to adjust their breeding date to climate change, because on the wintering grounds it is often impossible to predict changes in the onset of optimal reproductive conditions on the breeding grounds. They use internal clocks or cues such as day length to time the start of spring migration (Gwinner, 1996), and this constrains their adjustment to climate change (Both and Visser, 2001; Coppack and Pulido, 2004, this volume).

Up to now we discussed the cues in the environment of decision-making used by birds, and how these cues may facilitate or complicate the development of appropriate proximate responses to climate change. But reproducing females also have to gather large amounts of proteins to produce eggs and in early spring food resources are often limited. Often these resources for egg production are different from those used to raise nestlings. We need to know what resources females use during egg production and whether the phenology of these resources is affected by climate change. For instance, Dutch great tits provide their nestlings mainly with caterpillars from oaks

(*Quercus robur*) while, as far as we know, they use insects from birch (*Betula pubescens*) and larch (*Larix deciduas*) in the egg formation period. Oak bud burst is strongly temperature sensitive while birch and larch are not, and thus the interval between budburst of these species and that of the oak has become shorter over the past two decades (Visser *et al.*, 1998).

In conclusion, whether changes in the environment of decision-making will lead to changes in the timing of reproduction will vary among species. Opportunistic breeders are likely to be affected by climate change during the period of gonad development and egg formation, while species that migrate are less likely to be affected at that time. For resident species, the question whether changes in the environment of decision-making will lead to changes in the timing of reproduction will strongly depend on the importance of day length relative to other cues. As day length is not changing it is likely that in species in which this cue has an overriding effect, timing of egg laying will be affected to a minor extent.

B. Changes in the Environment of Selection

How a bird species should adjust its breeding date in response to climate change depends to a large extent on the response of other parts of the food chain during the time of selection. In a strongly seasonal environment that is affected by temperature dependent processes, we expect that the phenology of a large part of the ecosystem should advance in response to climate change. In temperate regions, invertebrates such as caterpillars consuming leaves of deciduous trees provide a good example (Buse *et al.*, 1999). Both tree and insect phenology are temperature dependent and only young leaves are palatable to most herbivorous insects eaten by birds. In general birds specialising on these insects produce only a single successful brood per season. To ensure successful reproduction, these single-brooded bird species should adjust their timing of raising chicks (breeding date) to advances in insect availability. However, once the birds have started egg laying, they cannot lay more than one egg a day, and are rather fixed in the duration of incubation and chick rearing (van Noordwijk *et al.*, 1995). Therefore, an increase in ambient temperature starting after the onset of egg laying will not lead to an advancement of the chick stage. By contrast, the development of tree leaves and their herbivorous invertebrates is strongly temperature dependent, and an increase in temperature after the start of egg laying in birds thus advances the peak in food availability without the birds being able to respond.

In environments with a less pronounced peak in food availability during the stage of chick feeding, and where species can raise more than one brood per season, the need to adjust breeding date to climate change may be less strong, although also in these environments individuals with multiple broods will have

the highest fitness and therefore should time their reproduction appropriately. Furthermore, a seasonal decline in offspring value is observed in many species (Nilsson, 1999 for a review) forcing birds to breed as early as possible. In several raptor species prey (rodent) populations steadily increase during the summer, but the seasonal decline in offspring survival selects for birds to breed as early as possible (Daan *et al.*, 1988, 1990). The need to advance breeding date in response to climate change is probably less in species relying on food sources for which the availability is not temperature dependent, such as granivorous species. Again, this depends on other date dependent effects on fitness of both parents and offspring, and competition for available food. In general we need to know the effect of climate change on development and availability of essential resources such as nestling food. Therefore, we need to develop a more multi-trophic approach including all underlying parts of the food chain to make a good prediction which species are most likely to be affected by climate change.

Ecological differences, even on a small spatial scale, can affect variation in the environment of selection and consequently how birds should be reacting to climate change. Blue tits on the island of Corsica breed in two very different types of habitats that are interspersed on short distance; evergreen and deciduous Oaks (Lambrechts *et al.*, 1997a,b; Blondel *et al.*, 1999). The phenology of the evergreen habitat (Pirio population) is a late bud burst and a late food peak. In contrast, the leafing of trees in the deciduous habitat (Muro population) and the food peak is much earlier. The blue tit populations in these forests are well adapted to these two species of oaks, with the Pirio population laying about 1 month later than the Muro population, even though these habitats are only 25 km apart. Given this long interval, it may well be that climate change will affect these two populations very differently. As suggested by Visser *et al.* (2003a) the populations in habitats with a late food peak, which also breed late, may escape from impacts of climate change either because they breed outside the seasonal window during which climate change occurs, or because the phenology of the entire food chain is less temperature sensitive. The latter explanation might be less likely as it has been suggested that there is no difference in temperature sensitivity in gonadal development between early and late breeding blue tit populations in the Mediterranean region (Lambrechts *et al.*, 1997, 1999).

In conclusion, the environment of selection is to a large part determined by food availability when chicks are in the nest. Climate change is expected to change the environment of selection for many species, but perhaps most strongly for species depending on a relatively short peak in resources. As the environment of selection strongly depends on the underlying levels of the food chain, including the vegetation, there may be very fine-scale spatial variance in changes in this environment.

C. Changes in Synchronisation

Great tits start their egg laying about 1 month before they need most food during the nestling stage, and the environments of decision-making and selection are thus separated in time. Both environments are not necessarily exposed to the same changes in climate, and such a differential change leads to a disruption in synchronisation between the nestling time and the time food availability is at its maximum. There is no *a priori* reason to expect that the time of egg formation in the environment of decision-making and the time and speed of insect growth in the environment of selection shift at the same rate in response to climate change. The phenology of the nestlings' food is determined by the underlying levels of the food chain, for instance by the vegetation. These organisms differ strongly from birds and are likely to have different response mechanisms to time their phenology and growth patterns. Especially the importance of the non-changing photoperiod cue is very different as it plays an important role in the response mechanism of many temperate zone avian species but hardly affects the timing of maximum insect availability. Although natural selection has favoured avian response mechanisms to lead to a similar advancement and delay in warm and cold spring as the phenology of the underlying tropic levels, it is important to realise that this only holds for the environment in which these response mechanisms have evolved. Thus, birds will react to cues that have predictive value of when the food peak will be, but these cues probably only work in a restricted climatic range and rely on a certain temporal structure in these cues. Problems arise when climate change shifts temperatures outside the normal range, and when some periods in the season are more affected than others (Visser *et al.*, 2003b).

Climate change may lead to differential changes in the breeding dates and the time of maximum food abundance. The breeding date may become later than the best time to rear the chicks, as discussed earlier, but birds may also advance more than the food peak. This phenomenon has been reported in the British great tit population of Wytham Wood, Oxford, England, where the birds advanced the egg laying date stronger than the peak time of their caterpillar prey (Cresswell and McCleery, 2003). This makes an interesting contrast with the Dutch great tit population on the Hoge Veluwe where there has been a shift in the peak date of caterpillar availability but not in the average onset of egg laying (Visser *et al.*, 1998, 2003b). As a consequence, there has been an increased selection for early laying in the Hoge Veluwe population, but not in Wytham Wood where selection on early laying has declined. Thus, the Dutch great tits responded too weakly to climate change while in the UK population the birds, which in the past always bred late relative to the food peak, now on average got better synchronised with their prey. This better synchronisation at Wytham Wood also gives the birds more flexibility to advance hatching in warm springs, and consequently the breeding success has increased over the years. As outlined above, there is no

a priori reason to expect that synchrony is maintained. Synchronisation may get better or worse, either because the phenology of the birds advances less or more than the phenology of the food they need. Why the one situation occurs in the UK population and the other in the Dutch population remains unclear. The explanation that in the UK temperatures in both the pre-laying and the breeding period has increased (Stevenson and Bryant, 2000) while in the Netherlands only the breeding period has become warmer (Visser *et al.*, 1998) was rejected in a comparison of laying date trends on a Europe wide scale (Visser *et al.*, 2003a) as within Europe there are areas where temperatures in the pre-laying period have not increased but laying date has advanced (two populations in Belgium and one in the Netherlands).

Another example of how climate change leads to mistiming comes from a long-distance migrant, the pied flycatcher. Long distance migrants may have even more difficulties in maintaining synchronisation with their food sources. They normally arrive at their breeding grounds only shortly before they start breeding, which constrains their ability to anticipate the advancement of their food sources. This was clearly observed in a Dutch pied flycatcher population that advanced its egg laying date by about 7 days reducing the time interval between arrival and laying (Both and Visser, 2001). Since the food peak in the same area advanced by about 2 weeks, the synchronisation between the nestling period and the food peak deteriorated, and as a consequence selection for early breeding increased (Both and Visser, 2001). The Dutch flycatchers thus advanced their laying date, but the rate of advancement was insufficient to track change in the environment of selection, and this is because their arrival date on the breeding grounds has not advanced, constraining their advancement in laying date.

IV. CONSEQUENCES OF REPRODUCTIVE MISTIMING

Mistiming will have consequences, both for the life-histories and population dynamics of birds. A clear example of the consequences of disrupted synchrony between realised and optimal breeding time is that food availability is lower for parents when feeding their young (Sanz *et al.*, 2003). Thomas *et al.* (2001a) have clearly demonstrated the negative consequences of such mistiming for parents. They measured metabolic effort of blue tit parents facing variation in prey availability during the chick stage (Figure 3). Especially in poor evergreen oak habitat in continental southern France, Blue tit parents face mismatching between nestling demand and prey availability, forcing them to increase foraging effort beyond their sustainable limit (Drent and Daan, 1980), thereby potentially influencing adult survival in these habitats. These negative consequences were not observed in a Corsican blue tit population that is nicely adapted to the same

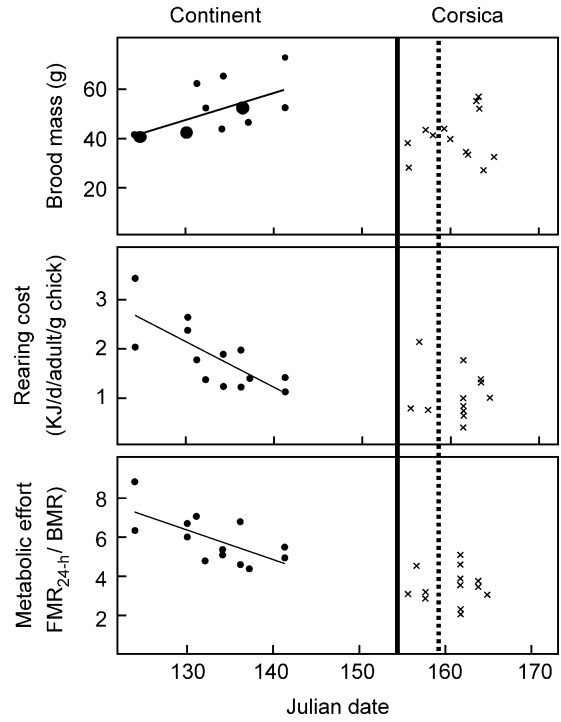

Figure 3 Consequences of mistiming in French blue tits: top panel gives the fledging mass of the offspring, middle panel the rearing cost for the parents and bottom panel the metabolic effort for the parents, all against the date at which the chicks are 8 days old (the age at which their need for food peaks). Symbols on the left hand of the graphs (•) are for a continental population, symbols on the right (x) are for a Corsican population. The grey lines represent the date at which the abundance of food used to rear the offspring peaks (solid line for the mainland, broken line for Corsica) (adapted from Thomas *et al.,* 2001a,b).

habitat type (Thomas *et al.*, 2001a), and are probably also less pronounced in very rich habitats with super abundant food (Thomas *et al.*, 2001b; Tremblay *et al.*, 2003).

The population consequences of mistiming in the Dutch flycatchers are clearly visible as a decline in population numbers in some, but not all habitats. During the last decades flycatchers breeding in nest boxes declined dramatically in rich deciduous forests, while no systematic trend was observed in mixed and pure pine forests (Both *et al.*, in preparation; Figure 4). This is because the food peak has become earlier and shorter in those rich deciduous forests, and flycatchers used to breed in this habitat during the declining phase of the food peak. The birds

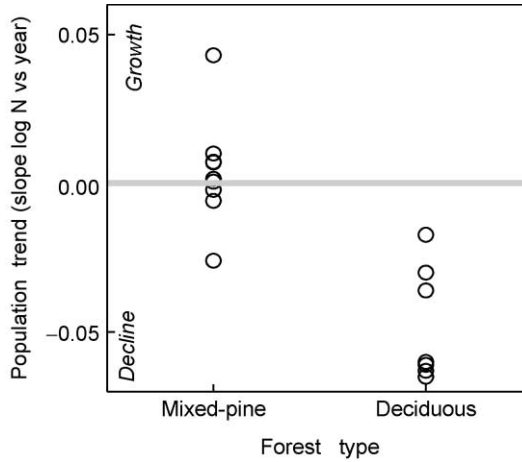

Figure 4 Changes in population numbers (slope of log population number versus year for 1987–2001) for 16 Dutch pied flycatcher populations in either mixed-pine or deciduous forests (adapted from Both *et al.*, in preparation).

however did not track the advancement of this food peak and as a consequence they now miss this food peak completely, and their numbers have declined. In mixed and pine forests the food peak is later and probably broader, and although the food peak has advanced here as well, the birds were better able to adjust their laying dates to this advancement. However, as we showed for the mixed forest of the Hoge Veluwe, the fitness landscape changed here as well, because the birds were unable to fully adjust their laying date to the advancement of the food peak. Since further adjustment to climate change in these flycatcher populations is constrained by their arrival time, we expect that birds also would miss the food peak in this habitat if the advancement continues, with similar population declines as now observed in deciduous habitats.

In the Dutch great and blue tit studies we do not yet see a decline in population numbers (unpublished results). This might be because winter food conditions have an overriding effect on population numbers, mainly via the survival probability for birds in their first winter (Perdeck *et al.*, 2000; Visser et al., submitted). One important food source in winter is beech mast, which occurs on average once every three winters, and drives the population dynamics of the tits to a large extent (Perrins, 1966). Interestingly, the amount of beech crop is predicted to increase over the next century as a consequence of climate change (van der Meer *et al.*, 2002), which might counteract the negative effect of disrupted synchrony. However, if the mistiming continues to increase then also for the tit species, there will be a moment when also the earliest birds hatch their

chicks too late to make use of the high but short peak in caterpillar biomass abundance, similar to what we have seen in pied flycatchers.

V. ADAPTATIONS TO REPRODUCTIVE MISTIMING

Given the negative consequences of reproductive mistiming it is important to assess the way individuals or populations can adapt to climate change. Here we will address whether birds can adjust other components of their life history to reduce the negative fitness consequences of mistiming (Section A), and whether populations will adapt to the changing environment and thus restore the match between the timing of maximal food requirements and the time of maximal food availability (Section B).

A. Responses of Individuals

In many bird species, individuals reproduce earlier in warm than in cold springs (Dunn, 2004, this volume). However, as we have argued above, climate change might lead to an insufficient advancement of laying date in these warm springs and the birds might be mistimed. After birds have laid their first egg, they have only limited possibilities for adjustment of hatching dates, which determines the mismatch between offspring needs and food abundance (van Noordwijk *et al.*, 1995; Wesolowski, 2000; Visser *et al.*, 2003b). One option is laying a smaller clutch to advance the hatching date with one or a few days.

However, often the opposite is found: when birds advance their laying date, they also lay a larger clutch (Winkel and Hudde, 1997; Winkler *et al.*, 2002; Both and Visser, submitted). This could be explained by inflexibility of the generally found decline of clutch size with laying date. However, as Both and Visser (submitted) show, this decline is not fixed but is for pied flycatchers steeper in warmer springs, because in those years a clear fitness cost of being late exists. Birds thus trade clutch size against hatching date in order to maximise their fitness (see also Dunn, 2004, this volume).

An alternative to advance hatching date for a given laying date is to reduce the interval between the last egg being laid and the start of incubation. Great tits (Visser *et al.*, 1998, 2003b) and pied flycatchers (Both and Visser, submitted) at the Hoge Veluwe (NL) have over the past two decades started to incubate incomplete clutches, thereby reducing the incubation period. It is likely that such an early start of incubation will come at a cost, as it will lead to hatching asynchrony, and perhaps to an increased mortality risk for the last hatched chicks. Interestingly, the great tits at Wytham Wood (UK) got on average better synchronised with the environment over the years and their incubation time has increased, resulting

in reduced hatching asynchrony and higher nest survival (Cresswell and McCleery, 2003). Rather than just using laying date to adjust hatching date, birds may use the whole complex of laying date, clutch size and start of incubation to advance the chick stage in response to climate change.

Birds may learn from previous experience and thereby adapt to disrupted synchrony with the environment. Great tits that hatched their chicks late relative to the peak in food abundance advanced their timing the next year (Nager and van Noordwijk, 1995). Learning the best breeding date is causally linked to experienced mistiming as shown experimentally in blue tits by Grieco *et al.* (2002). This learning mechanism may have evolved to cope with spatial and temporal variation in food phenology and birds may become better adapted during their life if the climate changes directionally. Although beneficial to the individual bird, in short lived species we predict that this learning effect will be insufficient to prevent the population from adverse effects of mistiming, because most birds are young and have no prior experience and hence lay too late.

In migratory species, the timing of arrival at the breeding grounds may hamper advancement of laying date (Both and Visser, 2001). Migrants may be able to advance their arrival date as the improved circumstances en route may speed these birds up to a certain extent, but this would only give a limited flexibility to climate change if the start of migration is very rigid (Coppack and Both, 2002). Most species of long distance migrants arrive at the breeding grounds some time before they start breeding in an average year, which gives them some flexibility to anticipate natural variation in the advancement of spring between years (Drent *et al.*, 2003). By reducing the time between arrival and breeding they can to a limited extent adjust to the advancement of the optimal breeding time caused by climate change. However, if arrival is not advanced, their adjustment to climate change is insufficient in the long term (Both and Visser, 2001). A change in migration schedule is therefore needed for adapting to a changing climate. This probably requires selection on the response mechanism for the onset of migration, and that the environmental conditions at the wintering grounds and en route allow earlier migration. Since climate change differs between latitudes this may constrain selection for earlier migration.

B. Population Responses

If food sources advance more than the birds' timing of breeding, early laying birds will increasingly produce more surviving offspring relative to late laying birds. This will lead to negative selection differentials for laying date (i.e., selection for earlier laying). The question is whether such increased selection will lead to changes at a population level such that mistiming will

be reduced. To answer this question we first need to establish where selection will operate. Selection for the timing of breeding operates not on laying dates as a genetically "fixed" trait, but on how an individual (or genotype) adjusts its laying date to environmental cues. This reaction norm or physiological response mechanism gives an individual the flexibility to adjust its laying date to the prevailing circumstances so that it lays at the approximate optimal date for a whole range of years differing in environmental conditions. It is important to realise that natural selection has shaped this mechanism for a specific set of abiotic variables (weather patterns). Global climate change is not only an increase in average annual temperatures, but temperatures in some periods increase more than in other periods of the year. As a consequence, climate change may disrupt the particular set of correlated environmental variables under which the physiological response mechanisms have evolved. This would be no problem if the lower levels of the food chain have the same physiological response mechanisms and are thus affected similarly as birds. However, they are likely to have other response mechanisms and are thus affected by different environmental variables. These different variables in turn might be affected differently by climate change (Visser and Holleman, 2001). It is therefore likely that under climate change the physiological response mechanisms underlying phenotypic plasticity in laying dates no longer accurately predict the timing of favourable conditions, and are thus no longer adaptive.

As the response mechanisms underlying phenotypic plasticity are no longer adaptive, the only way birds can adapt to these changes in climate is via selection on the shape of the reaction norm, i.e., on the genetic basis of phenotypic plasticity. This makes the debate on whether the observed advancement of laying date is due to phenotypic plasticity or a shift in gene frequencies of limited value (Przybylo *et al.*, 2000; Both and Visser, 2001). As reaction norms evolved for a limited range of environmental conditions, it is not the question whether animals can adapt either via phenotypic plasticity or via changes in gene frequencies, but much more via changes in the genetic basis of phenotypic plasticity (Visser and Holleman, 2001).

Synchrony could be restored by a change in gene frequencies of the response mechanism of laying dates to environmental circumstances (phenotypic plasticity). Such an evolutionary response is, however, only possible if egg laying date is heritable. There is some evidence for that (Merilä and Sheldon, 2001), but the conventional idea about heritability may not be very useful for a plastic trait like laying date that individuals alter depending on the environmental conditions that they encounter. Natural selection will operate on the response mechanism underlying this plasticity (see above and Coppack and Pulido, 2004, this volume). We only have a good idea how this mechanism is shaped for a few species, but we have no idea of variation in this mechanism even in these species, let alone whether this variation has a heritable component. To complicate matters

further, selection on plasticity of a character (on the reaction norm) is believed to be slow (van Tienderen and Koelewijn, 1994). This makes it unlikely that natural selection will be able to keep up with rapid changes in climate.

The response to selection also depends on the scale of climate change and on the extent of gene flow across local populations. Even on a small scale there is variation in the rate at which populations shift their laying date (Visser *et al.*, 2003a). There will be gene flow between some of these populations. An extreme example of contrasting selection pressures on a very local scale, over which dispersal can easily occur, is the blue tit on Corsica. Two populations that are only 25 km apart evolved pronounced differences in laying date in response to local optimal breeding time, which is assumed to have a genetic basis. This suggests that evolution in egg laying dates is possible even at a small spatial scale (Lambrechts *et al.*, 1997a,b; 1999; Blondel *et al.*, 1999), especially in conditions where selection pressures are predictable at the scale (e.g., landscape) of the dispersal range of the species.

Gene flow could, however, not only hamper adaptation but also allow new genes with different response mechanisms to enter the population and thereby broaden the range of phenotypes on which selection can act. We have limited evidence that there is spatial variation in the response mechanism, both on large (Silverin *et al.*, 1993; see Figure 2 in Coppack and Pulido, 2004, this volume) and small geographical scales (Lambrechts *et al.*, 1997a). While there may have been strong selection against gene flow in the past, as this counteracts local adaptation in the current situation of disrupted synchrony, selection may actually favour gene flow. Immigration of birds with different response mechanisms, some of which are now better adapted to the local situation than the residents, may allow populations to adapt to climate change (Coppack and Both, 2002).

VI. DISCUSSION AND CONCLUSIONS

Climate change is already apparent as an advancement of spring phenology. We argued in this chapter, however, that there is no *a priori* reason to expect that all components of food chains will shift their phenology at the same rate. The main reason is that the different components in a food chain will have different response mechanisms underlying the timing of their phenology and that apart from an overall change in temperature, there will also be a change in weather patterns (correlations between climatic variables, either in time or space). We may expect that under undisturbed weather patterns different response mechanisms of components in the food chain will be selected so that they shift more or less to the same degree with varying spring conditions. However, this expectation will no longer hold under novel weather patterns, simply because the mechanisms have not been selected under these new environments.

When different components of the food chain shift at different rates, this will lead to mistiming and we believe that such mistiming resulting from climate change will be a general phenomenon. If we now zoom in from this general picture to avian reproduction (Figure 2), birds seem to be especially vulnerable. The environment at the time they produce their eggs (environment of decision-making) is in general much earlier than the environment when selection will occur on for instance synchrony between offspring needs and prey availability (the environment of selection). The evolved response mechanisms are appropriate for the range of prevailing conditions, and climate change is a trend that will at first fall within the normal range of temperatures. In the short term, an increase in temperatures therefore may allow birds to cope with their existing reaction norms. If these temperatures fall outside the normal range, or if periods in spring differ in their temperature change, the prevailing reaction norms become maladaptive. Furthermore, the photoperiod (which is not affected by climate change) is an important component of the environment of decision-making for birds, but not of the environment of selection (see also Coppack and Pulido, 2004, this volume). As a result, birds are unlikely to advance their laying date at an appropriate rate.

There are only three studies that compared the actual shift in laying date with the one that would be optimal. Two of these (great tit, Visser *et al.*, 1998; pied flycatcher, Both and Visser, 2001) find that the shift in laying date is insufficient, despite the fact that there is a significant advancement of laying date in the pied flycatcher. The third (great tit, Cresswell and McCleery, 2003) finds that selection in the past favoured early laying birds, but that this early bird advantage declined with time, which may suggest that birds advanced more than their food source.

We have assumed almost throughout the entire chapter that birds respond to climate change by changes in their laying date solely. But for the pied flycatcher and we also investigated clutch size and onset of incubation (Both and Visser, submitted). We concluded that the pied flycatchers may, rather than just using laying date as a way to advance hatching date, use the whole complex of laying date, clutch size and start of incubation. Birds may also adjust other correlated life-history traits as some species show no change in laying date but do respond in whether or not they make a second brood (i.e., produce within a season a second brood after a successful first brood has fledged). In Northwest European great tit populations a dichotomy existed, with populations that did not advance their laying date reducing the proportion of second broods over time, while populations with a stable and low frequency of second broods advancing their laying date (Visser *et al.*, 2003a).

Birds may actually not just time when to start their first brood in a season but may be optimising the timing of their entire annual cycle. This is particularly likely as many life-history traits affect each other, like for instance reproduction and moult or autumn migration and moult (Coppack *et al.*, 2001).

For long-distance migrants this inter-dependence of timing of life-history traits is even more clear as their spring arrival date, and thus their spring departure date and migration speed, strongly limits their advancement of laying date and influences fitness consequences of mistiming (Coppack and Both, 2002). Thus viewing the impact of climate change on reproduction in isolation from other life-history events may be convenient but perhaps misleading. Species may respond to climate change, but in different life-history characters than timing of reproduction. Thus, when we compare species in their shift in laying date we might find that some of the non-advancing populations change a different life-history character. On the other hand, some of the advancing populations may not be doing so well at all if it turns out that they are advancing but not at the appropriate rate. This makes the interpretation of the meta-analysis on shifts in timing of avian reproduction difficult (Crick *et al.*, 1997; Crick and Sparks, 1999; Parmesan and Yohe, 2003; Root *et al.*, 2003).

Traditionally, birds were thought to time their breeding season so that the peak demand of the chicks matches the peak availability of prey used to feed the chicks (Lack, 1933). Although this synchronisation is indeed one of the major selection pressures acting on timing of reproduction, more recent studies have emphasised that also egg laying and incubation are costly, and therefore act as important selection pressures when a bird should lay (Monaghan and Nager, 1997; Stevenson and Bryant, 2000; Visser and Lessells, 2001). And as costs made in an early part of the reproductive cycle also affect costs in subsequent parts (Heany *et al.*, 1995), selection might operate on the entire reproductive cycle, or even on the entire life cycle when also timing of moult or migration is included, making it harder to identify the environment of selection.

Several important questions need to be addressed in future research on causes and consequences of climate change. A first outstanding question to be examined is whether our prediction that climate change will in general lead to mistiming holds. For this, more species should be investigated. Visser *et al.* (2003b) provide a number of methods to evaluate this: change in selection pressures on egg laying dates, direct measurements of changes in phenology of resources for offspring, and examination of behavioural responses such as an earlier in onset of incubation.

A second outstanding question is whether natural selection will lead to changes at the population level so that mistiming will be reduced. A prerequisite for this is that there is heritable variation in the response mechanisms birds use. We know very little about this, but a first step would be to document existing variation in response mechanisms within species having a wide geographic distribution (using any of the 75 species with a distribution from Scandinavia to Southern Europe), as Silverin (1995) (see Figure 2 in Coppack and Pulido, 2004, this volume) did for the great tit. If there is

sufficient geographical variation in response mechanisms, this indicates that species can adapt to a wide range of climatic conditions that is at least as large as the predicted changes in climate. This argument assumes that climate change will not lead to climatic conditions which fall clearly outside the existing range in climates encountered throughout the distributional range of species. We would predict that populations with a wide geographical distribution are better able to cope with climate change as they will have ample intraspecific variation in response mechanisms, so that dispersal across latitudes may allow rapid adaptation through changes in existing frequencies of response mechanisms. If selection would act on response mechanisms we would predict genetic change at the level of the response mechanism, and therefore need to estimate heritable variation in response mechanisms. As endocrinologists and quantitative geneticists have detailed knowledge of the processes underlying timing of reproduction, we advocate close collaboration between endocrinologists, geneticists and ecologists to unravel these response mechanisms, and its genetic basis.

A third outstanding question is the consequences of mistiming for population dynamics. We know very little about this at present except for recent work on the pied flycatcher in the Netherlands, where the populations are disappearing in rich oak forests (Both *et al.*, in preparation; see Section IV). Dunn (2004, this volume) discusses the effect of climate change on population processes such as fledging success but to what extent mistiming underlies the effects he reports is unknown. These questions are just starting to be addressed (Sæther *et al.*, 2004, this volume).

A final objective for future research is to increase our understanding of the effect of climate change on phenology for a number of species that differ in ecology. Currently, this is greatly hampered by our limited knowledge of on the one hand the causal mechanisms underlying laying date and on the other hand by our knowledge of exactly what the underlying selection pressures are. Knowledge of the causal mechanism (the response mechanism) is crucial, as this will indicate which changing environmental variables are relevant. It will also enable us to make predictions about how timing will change, if there are no genetic changes in the population, over the next century (using the International Panel for Climate Change predictions). Knowledge of selection pressures, including those on the birds' prey (thus using a multi-trophic approach), is also crucial as this enables us to assess to what extent laying dates should shift. Only when we have such a yardstick can we answer the question whether populations have advanced their laying date *sufficiently* to match the shift in the period of favourable conditions for reproduction rather than just *whether or not* a population has advanced. We predict, and perhaps fear, that in most cases we will find that the shift in laying date has not been sufficient and hence that climate change will have led to mistiming.

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